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This report results from a contract tasking University of Groningen as follows: The contractor will develop a detailed, configurable, digital computational model of the arthropod compound eye that is capable of providing a quantitative, numerical description of various steps of the signal processing pathway. The resulting model will be capable of modeling optical phenomena observed and measured in the insect compound eye. Previously published data and experiments conducted under this construct will be used in model development and validation.

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*Seventh and final report* (*January 2006*)

**[FY02-033] – Developing a detailed integrated optics computational model capable of quantitative descriptions and predictions of the image analysis performance of compound eyes**

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**Summary**

This is the final report of a three-year project supported by the EOARD. The aim of the project has been to contribute to a quantitative description of image processing by compound eyes. The main results of the performed research on three types of compound eyes are summarized, and a list of publications is appended.

**Introduction**

Compound eyes are the imaging systems of insects and crustaceans. These compactly built animal machines fulfill a variety of tasks essential for survival: find food, find mates, and avoid predators. Arthropods have developed many potentially useful sensors, which could be considered revolutionary if they were engineered for use in autonomous robots. The project is part of a long-term initiative to develop an advanced optical sensor, that is a multi-aperture seeker, motivated by detailed understanding of the arthropod (insect) compound eye.

From an optics point of view, flies have arguably the simplest compound eye. The fly eye is now well understood, notably due to the recent work performed in the early phases of the project. This knowledge base has provided a solid foundation for the study of the more complicated compound eyes of other invertebrate species to which we have shifted subsequently. For studying the simultaneous processing of spatial and spectral information, butterflies have great potential. This is firstly because of their large and accessible eyes, and secondly because they have developed a wide range of optical tools to achieve sophisticated image acquisition. Various butterfly species have most exquisite eyes with a vast structural as well as functional diversity. Our present research is mostly

concentrated on combined experimental and theoretical studies of butterfly eyes, so to develop and test quantitative models of visual imaging and information processing.

**Results achieved during the project period**

During the project period important progress has been realized by studying three different compound eye types: *i*) the neural superposition eyes of flies, *ii*) the apposition eyes of butterflies and crabs, and *iii*) the optical superposition eyes of moths and other insects and crustaceans.

Compound eyes are composed of numerous (several thousand) eyelets, so-called ommatidia, each having a facet lens and a crystalline cone, which together form the imaging dioptrics, and 8 or 9 photoreceptor cells, which are surrounded by screening pigment cells functioning as optical barriers for stray light. The light-sensitive apparatus of a photoreceptor cell, formed by the visual pigment molecules and the phototransduction machinery, which transforms absorbed light into an electrical signal, is packed in a special organelle, the rhabdomere. The set of rhabdomeres of an ommatidium is called the rhabdom. In fly eyes, the rhabdomeres are spatially separate cylinders, each acting as an optical waveguide. In bee and butterfly eyes, the rhabdomeres are joined into a fused cylinder, which thus acts as one functional optical waveguide.

The basic architecture of compound eyes is recognized in the apposition eye type, where each facet lens focuses incident light from a narrow spatial field into the fused rhabdom. In optical superposition eyes a large set (often several hundred) of facet lenses together relay light into one rhabdom. This occurs due to the special optics of the crystalline cones, which act as so-called lens cylinders, akin to SELFOC optical fibers, and the presence of a clear zone between the dioptrics and the rhabdom layer. In neural superposition eyes, an individual facet lens channels light into a number of spatially separate rhabdomeres, each of which receives light from a slightly different visual field. The different optics of the three compound eye types are reflected in different anatomical arrangements. Each of the specific eye types, as a front end of a sensitive imaging system, has certain advantages and disadvantages, which must be understood before attempting technical applications.

*Modeling the integrated optics of fly eyes*

The optical characteristics of the neural superposition eyes of flies have been analyzed in the first phase of the research period. A comprehensive wave-optical model has been developed, which was possible owing to extensive knowledge previously acquired in experimental optical as well as electrophysiological studies [1,2,5,6; the numbers in brackets refer to the list of publications at the end of this report]. The model includes the diffraction properties of the facet lenses, the waveguide properties of the rhabdomeres, and the spectral dependences of the absorption coefficient of the visual pigments. It has been demonstrated that the model quantitatively and accurately describes experimentally measured sensitivity spectra as well as angular sensitivities of fly photoreceptors [1, 5]. The model thus constituted a firm basis for the analysis of image processing by the set of photoreceptors in a fly compound eye. For instance, the model has provided insight into the robust optics of the integrated optical system of a fly facet lens and the rhabdomere optical waveguide, where the diameter of a facet lens is 20-30 μm and that of the waveguide is 1-2 μm. The model showed that it is rather uncritical where the entrance plane of the waveguide is positioned. It was generally assumed before that the tip of the waveguide should be precisely placed in the focal plane of the lens (focal distance ca 60 μm), but it appeared that the wave properties of light allow considerable play, some 10-20 μm, for maximal capture of incident light [1].

The model furthermore offered an explanation for some extraordinary optical properties of the compound eyes of the fruitfly *Drosophila*, perhaps the most intensely studied biological system [2]. This tiny fly has extremely small facet lenses with surprisingly short focal distances, but it still manages to see well. This is realized by accepting a slight loss in spatial resolution, while compressing the minute optical system into a very small space [2]. It is now also understood how the pupil mechanism, a light control system mediated by movable pigment granules, optimizes the angular sensitivity of the photoreceptors, depending on the average light intensity in the environment [5]. The model has in addition enabled the assessment of the sensitivity enhancement provided by the carotenoid derivative 3-hydroxyretinal, which acts as a unique antenna or sensitizing pigment in fly eyes [6]. In conclusion, we now have gained a quite complete

understanding of the optical factors that determine the spectral properties as well as the spatial acuity of fly eyes.

*Optics of butterfly eyes*

Subsequently to the fly eye, the optical and physiological characteristics of butterfly apposition eyes have been studied. The optics of these eyes is considerable more complicated than the optics of fly eyes. Firstly, the eye's visual waveguide, the rhabdom, contains at least three different types of visual pigment, and secondly, the crystalline cone, which forms together with the facet lens the dioptric system of an ommatidium, has a very concentrated gradient refractive index, and thirdly, there is a so-called tapetum below the waveguide, which reflects part of the propagated light back into the waveguide; this all makes an optical analysis quite difficult. Nevertheless, we have been able to develop a working computational model for the butterfly rhabdom. By adapting the model to specific butterfly cases, it could quantitatively describe the spectral sensitivities measured from different classes of photoreceptors in the papilionid *Papilio xuthus* as well as the cabbage butterfly *Pieris rapae* [7, 9, 10, 14]. Using essentially the same model, measured time courses of absorbance spectra that occur during light-induced photochemical conversions of the visual pigments in the butterfly *Polygonia c-album*, an exemplary case of nymphalid butterflies, were described, yielding the absorption spectra of the visual pigments and their photoproducts [4, 12].

Butterfly eyes are specifically challenging because several different optical methods are utilized to realize color discrimination. That at least is the working hypothesis resulting from several studies on butterfly vision. The papilionid butterflies have two types of spectral filters, realized by yellow- and red-colored pigments, that are located in clusters of granules surrounding the rhabdom waveguides. They shift the spectral sensitivities to longer wavelengths as well as create narrow spectral bandwidths [10]. This results, among others, in sensitivity spectra for a set of photoreceptors peaking in the red, which presumably enables the red sensitivity necessary for the butterflies to detect red flowers [10, 17]. Cabbage butterflies have elaborated the tuning of red receptors by installing two types of red pigment filters, resulting in two classes of red receptor with very narrow bandwidths, peaking in the red and deep-red wavelength range

[9]. Cabbage butterflies most likely also have an extremely sophisticated spectral discrimination system in the short wavelength range, as they exploit three classes of visual pigment, causing photoreceptors with maximal absorption in the UV, violet and blue; in virtually all other arthropods there are only two short-wavelength classes, UV and blue. Male cabbage butterflies have even pushed the variation in receptor type further, namely by modifying the violet receptor into a double-peaked blue receptor. This is achieved by recruiting a special blue filter [14].

The research on color receptor types has strongly stimulated an additional line of research, namely that on coloration methods of insect bodies, specifically of butterfly wings [8, 13, 15, 17]. Measurements on numerous butterfly species indicate that the sensitivity spectra of the visual photoreceptors are tuned to the wing reflectance spectra. This finding indicates that studies on sensors and their technical applications should be integrated with studies that characterize the objects that must be detected.

*Superposition eyes and their delicacies*

The optical superposition eye, the eye type utilized by nocturnal moths, has a special design. Each photoreceptor receives light via a set of multiple facets, which endows these eyes with a photosensitivity that is several log units higher than that of apposition eyes, because in the latter case only one facet lens channels light into a rhabdom. Many nocturnal or crepuscular active arthropods therefore use superposition eyes. The problem with this eye design is however that the acceptance angles of the photoreceptors are easily distinctly broadened compared to the acceptance angles of photoreceptors in apposition eyes. The proper focusing by a large set of dioptrical systems onto one rhabdom appears to be a tall order for the builders of real superposition eyes. The developmental process, which is of course under genetic control, must very precisely construct the crystalline cones and their refractive gradients in order to have perfect focusing optics. That appears not to be realized in most eyes, presumably because the necessary genetic effort would mean major investments for which there are inadequate returns. To understand this, one must consider that nocturnal animals have access to little light and thus must rely on temporal as well spatial integration (so-called pooling) to achieve a sufficient signal to noise ratio with their photoreceptors. Nocturnal eyes

therefore have photoreceptors with wide acceptance angles. Nevertheless a number of day-active moths with superposition eyes exist. Not only is their light sensitivity high, but their spatial resolution appears to be high as well.

In order to learn more about the potential imaging properties of optical superposition, as well as of their limitations, we have recently performed a number of optical studies on superposition eyes. This work has revealed some important misconceptions in the literature. Firstly, the existing geometric optical treatments have been incomplete, and they have failed to realize that superposition eyes essentially act as negative refractive index materials. A general optical framework of superposition eyes has been formulated [20]. Secondly, superposition eyes are assumed to be essentially limited by single facet lens diffraction, because of incoherence. A closer look shows that the studies that led to this concept have been inadequate. The conclusion instead is that partial coherence is a crucial factor in superposition eye imaging and that the only important source of imaging errors are the optical imperfections of the dioptrical elements: facet lens and crystalline cone [21].

Moth eyes are special in that the outer surface of the facet lenses is studded with nanosized protuberances, which together act as an impedance matching device. This so-called corneal nipple array (CNA) was discovered 40 years ago. (The CNA research received essential support from AF EOAR.) This work has since led to numerous technical applications, known as moth-eye devices, including the anti-radar stealth technology. We have developed an optical model that quantitatively estimates the effect of the corneal nipple array on reflectance [13, 16, 21]. Calculations show that the height of the nipples is the crucial factor that determines the surface reflectance. The benefit of the corneal nipple array for photosensitivity enhancement appears to be minor, but the array is extremely effective for reducing the reflectance and hence the visibility of the eyes and their owner.

*Radiation of the supported research*

Other investigators of compound eyes now use the developed wave-optical model of the integrated fly facet-lens and optical-waveguide system in their research. A notable example is the work by Lee and co-workers. They have created artificial compound eyes

with reconfigurable microtemplating, that is polymer replication of microlens patterns and formation of polymer waveguides, self-aligned with the microlenses via a self-writing process in photosensitive polymer resin (Lee LP, Szema R: Inspirations from biological optics for advanced photonic systems, Science 310:1148-1150, 2005; Kim JY, Jeong KH, Lee LP: Artificial ommatidia by self-aligned microlenses and waveguides, Optics Letters 30: 5-7, 2005). The research of the Lee team is a shining example of biomimetics that was inspired by both experimental and theoretical biophysical studies on compound eyes. It may be safely predicted that this line of applied science will further benefit from studies on real visual systems, in this case insect eyes.

The fundamental work on both compound eye vision and insect coloration, which has been supported by the EOARD, has become recognized by the community of insect vision investigators, as is demonstrated by the regular invitation to contribute reviews of this research for books and for scientific as well as popular journals [7, 10, 11, 13, 15, 17, 22], during the project period.

**Further activities**

Ric Wehling (from Eglin AFB) and Valerie Martindale (EOARD) made a site visit at 4 April 2005. Ensuing Ric and I visited the Zoology department of Cambridge University (Prof Simon Laughlin and Dr Jeremy Niven) where we gave talks and had discussions on Vision inspired machines and optical flight control.

I participated in a WOS meeting in Tucson, hosted by Ric Wehling, where I lectured on our work on 'Compound eye modeling' (13-15 April 2005).
I then visited Eglin AFB, and I delivered three lectures there:
- 'Insect compound eyes: sophisticated and ultralight visual systems',
- 'Understanding the insect retina by quantitative modeling: spatial and spectral properties of fly and butterfly eyes',
- 'Photonic crystals on the wing: sexy structural colorations in butterflies, beetles and damselflies'.

I delivered lectures related with the research reported here at a number of conferences and symposia, of which the most relevant are:

- Annual Meeting Finnish Physical Society (invited by Prof. M. Weckström), Oulu, March 2004,
- International Conference of Entomology, Brisbane, August 2004; I organized a session on Insect Vision, together with Prof E. Warrant (University of Lund),
- Symposium Insect Sensors and Robotics (invited by Prof. M.V. Srinivasan), Brisbane, August 2004,
- Workshop Interface Disorder in Nanosystems (invited by Prof. G. Palasantzas), Leiden, June 2005,
- C.N.R.S. – Jacques Monod Conference, Physico-Chemical Ecology Of Organisms (invited by Prof. J. Casas), Roscoff, September 2005.

**Appointments**

This research has been performed in collaboration with a number of students and two appointed researchers. A postdoc, Dr K.J.A. Vanhoutte, performed in 2003 a 3 months research period, when he worked at a computational imaging analysis program. He also finalized a photochemical study of butterfly visual pigments. Furthermore a PhD student was attracted. P. Pirih started in September 2004 for a 4 year period, to perform a study on butterfly color vision.

**Perspectives and conclusions**

The research reported here will naturally be continued. Knowledge of the complicated interaction of spatial and spectral elements that determine spatial and color vision of insects and crustaceans is still quite incomplete. Further study is necessary to pinpoint the crucial factors for optimal vision with apposition eyes. Butterfly eyes will stay to be a rich source for research leading to novel insights. As noted above, some technical applications have already been attempted, but this approach is still in its infancy.

The insight into the critical points of superposition eyes that has recently been achieved will quite likely facilitate the nano-optical manufacturing of artificial superposition compound eyes, as has been realized already for the artificial apposition

eyes. The support provided by the EOARD has been instrumental for achieving the results presented here. The sponsoring is gratefully acknowledged.

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